Interactive aggregation and sedimentation of diatoms and clay-sized lithogenic material

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Abstract

Monospecific diatom cultures (*Thalassiosira punctigera* and *Skeletonema costatum*) were incubated in rotating cylinders together with clay suspensions, present in a range of concentrations (5–100 mg kaolinite L^{-1}) and as different minerals (50 mg L^{-1} kaolinite, smectite, illite, and clay-sized quartz powder). The addition of lithogenic suspensions to diatom cultures accelerated the formation of visible aggregates in the roller tanks by a factor of >3. Aggregate size decreased and density increased proportionally to the amount of kaolinite added to the diatom cultures. In the presence of kaolinite and illite, aggregate sizes were smaller and sinking rates lower than in the presence of smectite and quartz. The influence of lithogenic matter on the sinking velocities of aggregates was ambiguous. Compound aggregates sank faster with increasing amounts of lithogenic matter present in cultures of *T. punctigera* until a certain ratio between lithogenic and biogenic material was reached; further increasing the amount of lithogenic matter did not increase sinking rates significantly. In contrast, increasing the concentration of kaolinite added to cultures of *S. costatum* could decrease sinking velocities of the evolving compound aggregates. This nonlinear behavior is argued to be primarily a function of aggregate composition on aggregate sizes and excess densities. Although the possibility of a mutual acceleration of vertical flux of algae and clay is confirmed, the results show that the presence of lithogenic material could also decrease the downward flux of phytoplankton biomass.

Rapid sinking of phytoplankton-derived organic carbon via sedimentation of aggregates contributes significantly to the vertical transport of marine particulate organic carbon (POC), a process known as the biological pump (Volk and Hoffert 1985). Rapid sinking of clay-sized lithogenic material can be inferred from sediment trap data (Wefer 1989). Laboratory studies on marine aggregate formation and properties have focused on pure phytoplankton aggregates (Kiørboe et al. 1990; Riebesell et al. 1991; Kiørboe and Hansen 1993) or on monomineralic clay aggregates (Kranck 1973). However, coaggregation of phytoplankton and clay is a familiar phenomenon in aquatic environments. First drawings of marine snow show sundry marine organisms and mineral grains embedded in a mucous matrix, which dominates the aggregates by volume and appears to hold the solid compounds together (Tsujita 1953). Avnimelech et al. (1982) described enhanced floc formation and sedimentation of freshwater algae in the presence of clay and vice versa. The fact that lithogenic and biogenic particles are often found in deep sediment traps during the same time interval in spite of independent occurrence in the surface water also suggests coaggregation and cosedimentation of these particles (Deuser et al. 1983; Wefer 1989; Ittekkot 1993).

While small amounts of both biogenic and lithogenic particles are present in all marine environments, areas with elevated concentrations of lithogenic particles often show a high phytoplankton abundance at the same time and are thus particularly interesting in terms of interaction between phytoplankton and lithogenic material. Examples for marine environment with such properties are rivers plumes (Cadée 1984; Milliman and Meade 1983), shallow shelf areas (Hill and Nadeau 1989), areas with Aeolian input of lithogenic matter (Glaccum and Prospero 1980), and ice edges, especially those where sediment-rich ice (dirty ice) is melting (Nürnberg et al. 1994).

Summarizing evidence on coaggregation and cosedimentation, Cloern et al. (1983) and Degens and Ittekkot (1984) hypothesized that lithogenic material increases density and thus the sinking rate of phytodetritus aggregates. Ittekkot (1993) proposed an increased efficiency of the biological pump due to faster sinking of aggregates and of fecal pellets containing lithogenic material. Conversely, mutual aggregation of algae and clay was shown to result in the removal of clay from suspension (Avnimelech et al. 1982).

General predictions on particle size and density difference of mixed phytoplankton/clay aggregates can be made on the basis of models on aggregation and knowledge on material properties. As shown by a model by Riebesell and Wolf-Gladrow (1992), aggregate sizes crucially depend on particle size, stickiness, form, and concentration. Even though there are material-related differences between different clay-sized lithogenic minerals, particle size and stickiness are generally so low that even at high particle concentrations, aggregates remain small. The comparatively simple forms of lithogenic particles are not known to favor aggregate formation. Phytoplankton and associated mucus, on the other hand, can be large and sticky and can produce large aggregates if concentrations are sufficient. Chain-forming phytoplankton aggregate particularly well (Riebesell and Wolf-Gladrow 1992).

If algae and clay-sized lithogenic particles cooccur, intermediate sizes can be expected for evolving aggregates because the large, highly sticky surfaces of phytoplankton and associated mucus will be saturated by small clay particles, which have a lower stickiness and will destabilize the aggregate. Since densities of mixed aggregates directly result

Table 1. Composition of the suspensions used for roller tank incubation.

Experiment	Diatom species	Chl a (μg L^{-1})	POC (mg L^{-1})	Cell concentration (cells L^{-1})	Lithogenic matter (mg L^{-1})	Duration of incubation (d)
1	*Skeletonema costatum*	17.5	0.89	2.6×10^6	0, 5, 10, 20, 50 kaolinite	7
2	*Thalassiosira punctigera* diameter ca. 90 μm	70	1.91	1.6×10^5	0, 5, 10, 20, 50, 100 kaolinite	7
3	*Thalassiosira punctigera* diameter ca. 50 μm	70	1.97	3.9×10^5	50 kaolinite, illite, smectite, and quartz	3

from the densities of biogenic and lithogenic particles and the percentage (v/v) these particles occupy in the aggregate, they can be expected to have a higher density than phytoplankton aggregates and a lower density than clay aggregates. Thus, smaller sizes and higher densities of mixed aggregates compared to pure phytodetritus aggregates can be inferred. However, further predictions on changes in sinking rates (e.g., based on Stoke's equation) are difficult because the sinking rate of mixed aggregates increases only if $\Delta\rho r^2 > 1$, i.e., the excess density $\Delta\rho$ increases more than the square of the radius, r, decreases. Additionally, effects causing changes in form resistance and deviations from the conditions in which Stoke's Law may be used are not predictable. Therefore, experiments with coaggregated algae and clay, as described in the present study, are necessary to evaluate the influence of lithogenic particles on sinking velocities of phytodetritus aggregates.

Material and methods

Thalassiosira punctigera and *Skeletonema costatum* were cultured in enriched seawater medium (Drebes 1966). The Chl a content (measured according to Evans et al. 1987) in the diatom cultures prior to roller tank incubation had just reached its maximum, indicating transition from the exponential to the stationary phase. Particulate organic carbon (POC) was measured after filtration on GF/C filters using a Carlo Erba Autoanalyzer (CHN 1500), with acetanilide as a standard, to ensure comparability of the different alga suspensions used.

Typical marine lithogenic particles quartz, kaolinite, illite, and smectite, with specific surface areas of 2.65 m^2 g^{-1}, 14.2 m^2 g^{-1}, 94.4 m^2 g^{-1}, and 82.3 m^2 g^{-1}, respectively (measured as described by Brunauer et al. 1938), were used in the experiments. Cation exchange capacities (CEC) of these clay minerals, an indirect measure of surface charge, are typically 0.03–0.15 meq g^{-1} dry weight (kaolinite), 0.2–0.5 meq g^{-1} dry weight (illite), and 0.7–1.3 meq g^{-1} dry weight (smectite) (Scheffer and Schachtschabel 1992).

A series of increasing concentrations of kaolinite were added to suspensions of *S. costatum* and *T. punctigera* to study the influence of the amount of lithogenic material on aggregate formation and properties (experiments 1 and 2, Table 1). Fifty milligrams per liter of each typical marine lithogenic mineral were incubated with a suspension of *T. punctigera* (experiment 3, Table 1). Compound clay/phytoplankton aggregates from suspensions containing diatoms and clay-sized lithogenic particles were produced using

transparent cylindrical tanks (d = 20 cm, 5 turns min^{-1}, volume 1.6 liters) rotating on a roller tables (modified after Shanks and Edmondson 1989). In our lab, seven tanks could be kept in motion at one time.

No visible aggregation occurred within the first 12 h in the treatments containing only phytoplankton. Photographs were taken every 24 h to monitor aggregate formation and size development. The volumes of 20 randomly chosen aggregates >0.25 mm were assessed based on the photographs of each of the treatments under the assumption that they were either spherical, or rotational ellipsoids.

After 7 d for the experiments with increasing concentrations of kaolinite and 3 days for the experiment with different lithogenic materials, aggregates were present in all treatments containing phytoplankton. Individual aggregates were sampled by syringes, which had been cut so that the opening consisted of their whole inner diameter (d = 6 mm). Except for aggregates in the treatments containing *T. punctigera* and 100 mg kaolinite L^{-1} and *S. costatum* and 50 mg kaolinite L^{-1} intact aggregates were obtained. Individual aggregates were then transferred from the syringe to 40 × 80 × 40 cm (breadth × length × depth) transparent tanks containing water of the same salinity and temperature as the roller tanks. During sinking, time was measured every 5 cm (intervals were marked on the tank walls with circumferential black lines). Aggregates, which broke or lost material during sinking, were not used. After the sinking rate was measured, the whole aggregates were individually sampled by syringe from the bottom of the tank, whose water was virtually cell free. The syringe was attached to a glass rod; its piston was drawn up with a rope led through a glass tube. The aggregates were transferred to glass vials and shaken with a few milliliters of filtered seawater, which caused complete disintegration of the aggregates. The resulting cell suspension was transferred to Utermöhl chambers, where cells per aggregate were counted (Utermöhl 1958). From the relation between the average cell number of 7 to 15 randomly picked individual aggregates and the average volume of 20 randomly chosen aggregates measured in the roller tanks, the exponent x from the equation $d = N^x C$, where d is aggregate diameter (μm), N the cell number, and C the cell diameter (μm), was calculated and used to evaluate the size of individual aggregates. The exponent x is also a relative measure for the density of phytoplankton cells within the aggregates.

This procedure could not be used for the aggregates containing the chain-forming *S. costatum*, since their cells could not be separated and thus could not be counted properly. To get an estimate of aggregate sizes prior to measuring their

sinking velocities, diameters of aggregates containing *S. costatum* were measured with the scale on the 6-mm wide 1-ml syringes used for transfer (ticks were spaced at 0.55 mm).

As a first approximation, density difference to the surrounding sea water (excess density) was calculated from aggregate size and sinking velocity using Stoke's equation (Smayda 1970):

$$\Delta\rho = (\rho_{\text{aggregate}} - \rho_{\text{medium}}) = \frac{v_s 9 \eta \Phi}{2 g r^2}$$

where $\rho_{\text{aggregate}}$ and $\rho_{\text{sea water}}$ are the densities of the aggregate and the sea water, g is the acceleration due to gravity (9.81 m s^{-2}), η is the dynamic viscosity of the sea water used (1.4 $\times$ 10^{-3} kg m^{-1} s^{-1}), r is the aggregate radius, and v_s is the sinking velocity (10^{-3} m s^{-1}) of the aggregate. The form resistance Φ was assumed to be constant and was thus not considered here.

To evaluate whether differences were significant, the student *t*-test and a modified *t*-test were used to compare treatments with differing sizes of random samples (Sachs 1984) ($p = 0.05$). Sample sizes used for measuring sinking velocity ranged between 7 and 15 aggregates per treatment. On the roller table six tanks could be operated at a time. As aggregate properties were expected to be functions of the incubated material, with little chaotic influences and thus little variability between tanks containing the same particle compositions, six (instead of three in duplicate or two in triplicate) treatments with differing concentrations or qualities of lithogenic matter were used in each experiment. Table 1 depicts composition and properties of the material used for the experiments.

Results

In all experiments, aggregate formation in the roller tanks was accelerated when phytoplankton and clay cooccurred. In the suspensions containing both lithogenic and biogenic matter, aggregates were produced in less than 3 h, while in the pure phytoplankton suspensions, the first aggregates were observed after 3–5 d (Fig. 1). The pure kaolinite suspension showed no visible aggregates even after 1 week of incubation in the roller tank. The developments of aggregate sizes in the roller tanks were inconsistent. While in the experiment with *S. costatum* and kaolinite, aggregate sizes did not vary much once they had evolved (Fig. 1a), the treatments containing *T. punctigera* and ≥10 mg kaolinite L^{-1} formed relatively large aggregates after 24 h and showed a steady decrease of aggregate size with time (Fig. 1b).

By the time aggregates were sampled to measure sinking velocity, average aggregate sizes in the roller tanks were inversely related to the amount of kaolinite added. In the experiment with *S. costatum* and kaolinite aggregates ranged from over 300 mm³ for a single *S. costatum* aggregate in the treatment without lithogenic matter (which broke due to sampling, fragments were used to measure sinking velocity) to 0.2 mm³ for the treatment containing 50 mg kaolinite L^{-1} (Fig. 1a). In the experiment with *T. punctigera* and kaolinite, average sizes ranged from 4 mm³ for pure *T. punctigera* aggregates to 0.3 mm³ for the aggregates formed in the pres-
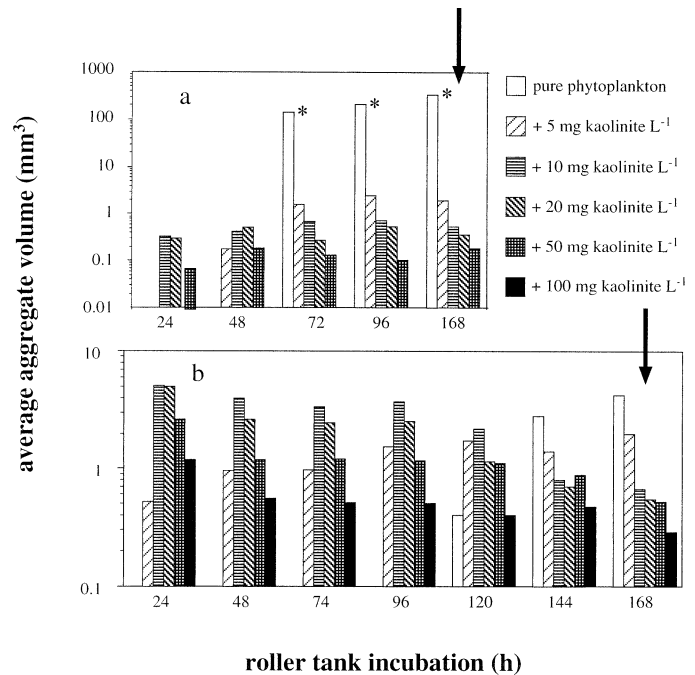

Fig. 1. Aggregate volumes as functions of initial particle compositions and time during the roller tank incubation (a) *Skeletonema costatum,* (b) *Thalassiosira punctigera* and diverse concentrations of kaolinite. The asterisks label a single, very large aggregate, the arrows indicate the time when sinking velocities were measured.

ence of 100 mg kaolinite L^{-1} (Fig. 1b). In contrast, the numbers of aggregates were positively correlated to the concentrations of lithogenic matter added.

The density of the aggregates increased as a function of the amount of added lithogenic material and was inversely related to aggregate sizes (Fig. 2 g–k; a–c). Excess density $\Delta\rho$ ranged from <1 mg ml^{-1} for pure phytoplankton aggregates to >100 mg ml^{-1} in mixed aggregates. Pure clay has an excess density of ca. 1,500 mg ml^{-1} in seawater. $\Delta\rho$ was thus the parameter that reacted most sensitively to the addition of lithogenic material. Even relatively low concentrations of kaolinite added (5 mg L^{-1}) increased the excess densities of the evolving aggregates by factors of 2–4. With increasing amount of kaolinite, the percentage volume *T. punctigera* cells occupied in the aggregates tended to decrease. The exponent x from the equation $d = N^x C$, where d is aggregate diameter (μm), N the cell number, and C the cell diameter (μm), was 0.433, 0.423, 0.492, 0.512, and 0.672 for the treatments containing 0, 5, 10, 20, and 50 mg L^{-1} kaolinite.

In the experiments with increasing concentrations of kaolinite incubated diatoms, the treatments containing the highest amounts of kaolinite (50 and 100 mg L^{-1} for *S. costatum* and *T. punctigera,* respectively) produced aggregates so small and fragile that sinking velocities could not be measured with the method used here. Likewise, the sinking velocity of the single large aggregate formed in the pure *S. costatum* suspension could not be measured, since it broke during the collection. Sinking velocities of aggregates from the incubation of *S. costatum* with 5 and 10 mg kaolinite
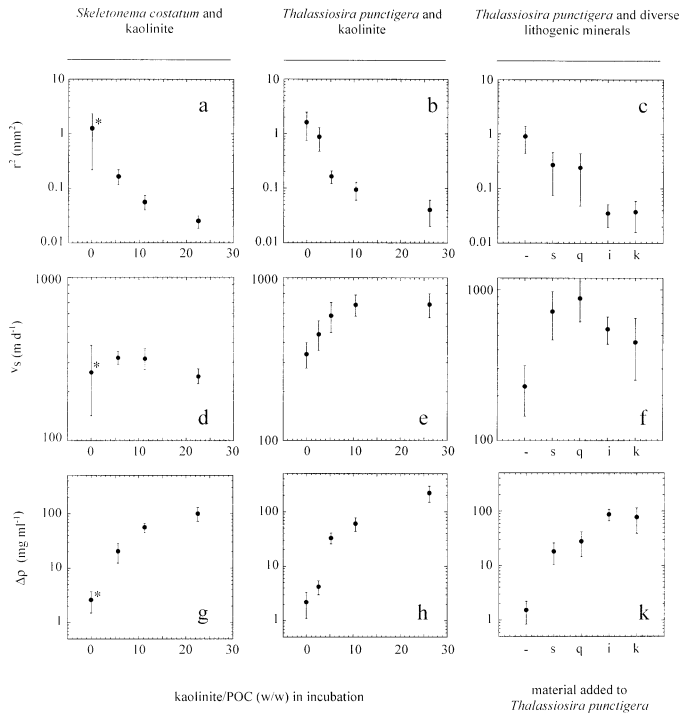
Fig. 2. Aggregate sizes, excess densities, and sinking velocities as functions of initial particle compositions in the roller tanks. (a)–(c) aggregate sizes (r^2). (a) *Skeletonema costatum* and kaolinite, (b) *Thalassiosira punctigera* and kaolinite, and (c) *Thalassiosira punctigera* and diverse lithogenic minerals (s, smectite; q, quartz; i, illite; k, kaolinite; —, control). (d)–(f) sinking velocities (m d^{-1}). (g)–(k) excess densities ($\Delta\rho$) as functions of initial particle concentrations. Panels d, e, and f and panels g, h, and k are the same treatments as panels a, b, and c, respectively. The asterisks label measurements and calculations depending on fragments of a larger aggregate. Note that sinking velocities are directly related to the product of $\Delta\rho$ and r^2.

L^{-1} added did not differ significantly. They reached average values of 323 and 319 m d^{-1}, respectively, whereas aggregates from the incubation containing 20 mg sank significantly more slowly (249 m d^{-1})(Fig. 2d). A significant increase of sinking velocities with increasing concentrations (0, 5, 10, and 20 mg L^{-1}) of kaolinite was observed in the experiment with *T. punctigera* (339, 449, 584, and 682 m d^{-1}, respectively). Sinking velocities of aggregates produced in the incubations with 50 mg L^{-1} kaolinite (684 m d^{-1}) were not significantly different from those of aggregates produced with 20 mg L^{-1} kaolinite. In the experiment with *T. punctigera* and diverse lithogenic materials, the aggregates formed by *T. punctigera* and quartz sank most quickly (860 m d^{-1}), followed by the treatments containing smectite (720 m d^{-1}), illite (560 m d^{-1}), kaolinite (480 m d^{-1}), and *T. punctigera* without clay (230 m d^{-1}).

Discussion

The effects lithogenic material had on sinking rates of phytodetritus aggregates were not linear, and the experiments described here do not reveal a straightforward influence of

the presence of lithogenic material. Several uncertainties resulting from the methodological approach prevent the results from being used as a basis to precisely calculate and predict sinking rates of aggregates containing algae and clay. Aggregation in roller tanks as used in this study tends to result in denser, more compact aggregates than does aggregation in the field. The calculation of aggregate densities is only a first approximation, since Stoke's law gives only an estimate for porous, quickly sinking aggregates. In addition, the measured and calculated aggregate sizes are approximations. However, the study revealed several fundamental effects of the presence of lithogenic material on formation and properties of phytodetritus aggregates.

Faster formation of aggregates in roller tanks containing fine lithogenic particles and phytoplankton suspensions is mainly due to increased collision probability (McCave 1984; Jackson 1990). Whenever the lithogenic particles stick to biogenic material, they increase their specific weight and thus their sinking velocity, which in turn leads to an increased collision probability with slower sinking particles. In environments with less shear, such as those in the roller tanks, cells alone do not aggregate as readily because of their low sinking rates and thus low collision rates. Lithogenic particles alone lack stickiness to form larger aggregates. Thus, enhanced aggregation in the mixed treatments, as shown in Fig. 1, was expected. In situ, shear can become very important in inducing collisions and aggregation of particles (McCave 1984). The shear-induced collision rates between larger particles will not be changed directly by addition of fine lithogenic particles. However, in the presence of fine lithogenic material, shear will induce additional collisions between biogenic and lithogenic particles, which accelerates the aggregation process due to differential settling.

In the presence of phytoplankton, mucous particles, or transparent exopolymeric particles, TEP, are more or less associated with phytoplankton cells and are an important particle class promoting the formation of phytodetritus aggregates (Alldredge et al. 1993; Passow et al. 1993). Such biogenic mucus and clay minerals have several properties in common. Both have high specific surface areas, carry negative charges (Decho 1990; Scheffer and Schachtschabel 1992), and can aggregate into larger units by forming cation bridges (Kranck 1973; Decho 1990). A coaggregation of both particle types in seawater, which contains high concentrations of cations, has been predicted (Degens and Ittekkot 1984). However, in the present study, quartz, though having less reactive surface properties, was also effectively incorporated into the aggregates. Fig. 3 illustrates that most lithogenic particles are only indirectly attached to diatom cells (i.e., most likely attached via mucoid particles).

The difference in aggregate size development between the experiment with *S. costatum* and kaolinite, where aggregate size remained relatively constant over time, and the experiment with *T. punctigera* and kaolinite, where aggregate size in the treatments containing ≥10 µg kaolinite L^{-1} decreased with time (Fig. 1 a,b), may be caused by the different properties of the phytoplankton used. *S. costatum,* known to form chains and to produce threads of mucus (Kiørboe and Hansen 1993), probably formed aggregates where sticky surfaces were soon saturated by kaolinite. *T. punctigera,* on the other
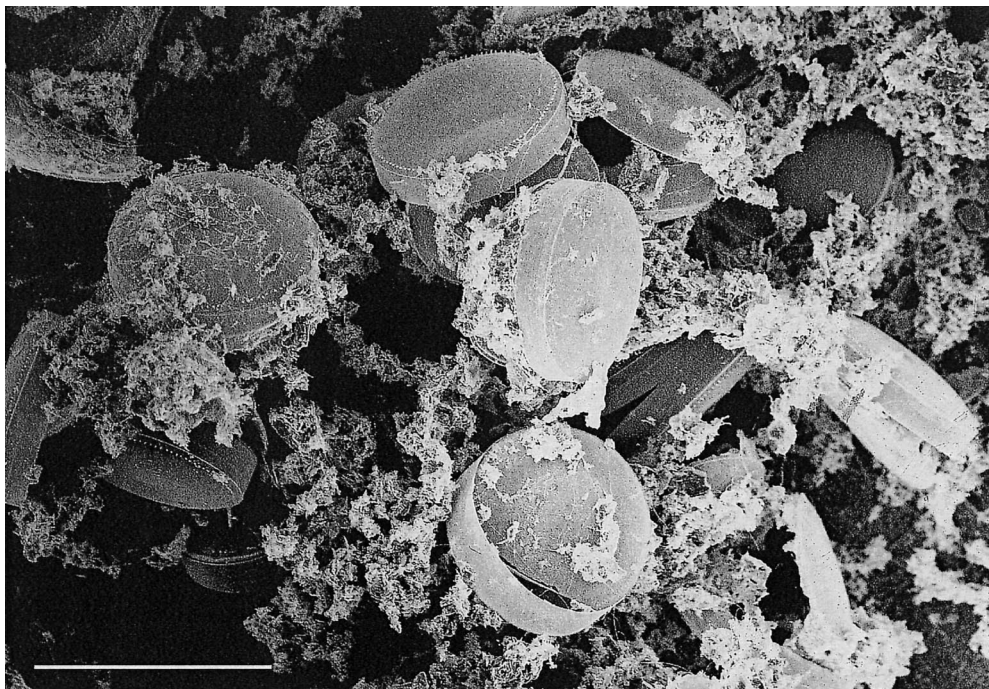
Fig. 3. SEM image of an aggregate from the treatment of *Thalassiosira punctigera* and 20 mg kaolinite L^{-1}. Note that most of clay particles are not directly attached to the diatom cells, but form clusters, which are probably bound by an extracellular organic material. Scale bar = 100 μm.

hand, may have produced more voluminous TEP and thus more sticky surfaces (Passow, pers. comm.), which were only gradually saturated by lithogenic material. This process would explain gradually decreasing aggregate sizes.

In the experiment with *T. punctigera* and diverse lithogenic materials, the addition of quartz and smectite led to the formation of rather large aggregates (average cell numbers/aggregate: 877 and 1,181, respectively). Illite and kaolinite, which were added in the same amounts, caused the formation of significantly smaller aggregates (average cell numbers/aggregate: 192 and 198, respectively). These similarities between smectite and quartz phytoplankton aggregates were unexpected at first sight because the quartz and the smectite used had the largest differences in two properties, crucially influencing the aggregation process. While the specific surface area of the quartz used is comparatively small, it virtually has no surface charge. Smectite has a large specific surface area and is known to have a high cation exchange capacity, indicating a high surface charge.

Potentially, the comparatively small specific surface area of the quartz used in the experiment saturated the sticky surfaces on the aggregates less efficiently than did the larger surfaces of the clay minerals, which may have resulted in the formation of relatively large aggregates. Fine lithogenic material, on the other hand, also produces large aggregates with phytoplankton if the lithogenic matter itself has specific properties, such as a high surface charge in the case of the smectite used. This may have caused a higher stickiness and thus a stabilization of the aggregates. This concept is also consistent with the fact that the lower surface charges of illite and kaolinite caused, in combination with their high specific surface areas, the formation of much smaller aggregates with phytoplankton.

Density differences of aggregates increased as a function of lithogenic matter added, which suggests efficient incorporation of lithogenic matter into aggregates. In contrast to the proportional effect that the mixing of compounds with different adhesion properties and densities had on aggregate sizes and densities, respectively, sinking rates of composite phytoplankton lithogenic matter aggregates can exceed the sinking velocities of both pure phytoplankton aggregates and aggregates composed only of lithogenic matter. Assuming constant form resistance, r^2 and $\Delta\rho$ are the main particle properties that determine, over their product, the sinking rate of an aggregate. This implies that in the experiments with *T. punctigera,* by increasing the concentration of lithogenic matter in the roller tanks, the density difference of the evolving aggregates initially increased faster than the square of their radius decreased (Fig. 2). Balancing increases and decreases of these parameters occurred when very high ratios of lithogenic matter/POC were used, which resulted in stagnating sinking velocities. In the experiment with *S. costatum* and kaolinite, the highest concentration of lithogenic matter even led to a decrease of sinking velocities of the evolving aggregates in spite of the increase in density difference (maximal ca. $100\times$), since this was counteracted by decreasing aggregate sizes. This effect is consistent with observations from areas with extremely high concentrations of lithogenic material, such as estuaries or tidal flats, where aggregate sizes are extremely small and their sinking rates very low (e.g., Dyer et al. 1996).

The experiments of the present study confirmed that lith-

ogenic particles aggregate efficiently with POC and may significantly increase the sinking rate of the produced aggregates. This corresponds to the considerations of Honjo (1982) and Ittekkot (1993), who predicted an increase in sinking velocities due to incorporation of lithogenic particles into phytodetritus aggregates. Assuming that degradation rates will not increase significantly, faster sinking of such aggregates, caused by the presence of lithogenic particles, would lead to a remineralization of POC in deeper zones, which in turn would increase the efficiency of the biological pump (sensu Ittekkot 1993). However, depending on types of biogenic and of lithogenic materials and the percentages they contribute to the compound aggregates, lithogenic particles may as well decrease the sinking velocity of phytodetritus aggregates.

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